

COURTSHIP DISPLAYS AND NATURAL HISTORY OF SCINTILLANT
(*SELASPHORUS SCINTILLA*) AND VOLCANO
(*S. FLAMMULA*) HUMMINGBIRDS

CHRISTOPHER J. CLARK,^{1,3} TERESA J. FEO,¹ AND IGNACIO ESCALANTE²

ABSTRACT.—The natural histories of Volcano (*Selasphorus flammula*) and Scintillant (*S. scintilla*) hummingbirds are poorly known. We describe aspects of their breeding behavior with emphasis on courtship displays and sounds that males produced for females. Males of neither species sang undirected song. Males of both species produced a display dive, in which they ascended ~25 m in the air and then dove, swooping over the female. Both species produced a pulsed sound that was synchronized with abrupt tail spreads during the bottom of the dive. The second rectrix (R2) of both species was capable of generating the same sound in a wind tunnel, suggesting these sounds were made by the tail. The dive sounds of the Volcano Hummingbird were louder than those of the Scintillant Hummingbird. Male Scintillant Hummingbirds produced a wing trill in flight, and performed a shuttle display to females in which the wing-beat frequency reached ~100 Hz. Males held territories in open areas during the breeding season. Not all territories included abundant floral resources, and abundant resources in closed habitat were not defended. The role of resources is unclear in the breeding system of these two species. Received 6 May 2010. Accepted 1 December 2010.

The basic natural history of most Central and South American species is poorly known, compared to North American birds. For example, of the seven species in the hummingbird clade *Selasphorus*, courtship displays consisting of both dives and shuttle displays have been described for Allen's (*S. sasin*) (Aldrich 1938, Mitchell 2000), Rufous (*S. rufus*) (Calder 1993, Hurly et al. 2001), and Broad-tailed (*S. platycercus*) (Calder and Calder 1992) hummingbirds, as well as Calliope Hummingbird (*Stellula calliope*) (Tamm et al. 1989, Calder and Calder 1994), which is phylogenetically nested within *Selasphorus* (McGuire et al. 2007, 2009). These four species breed in the United States and Canada. In contrast, courtship displays for Volcano (*S. flammula*) and Scintillant (*S. scintilla*) hummingbirds of Costa Rica are only known from the brief descriptions by Stiles (1983), and are entirely unknown for the Glow-throated Hummingbird (*S. ardens*) of Panama.

Members of *Selasphorus* and the related genera of *Calypte*, *Archilochus*, and *Mellisuga* perform dynamic and spectacular courtship dives (Clark 2006, Clark and Feo 2008, Feo and Clark 2010). *Selasphorus* and *Archilochus* also produce shuttle displays for females (Banks and Johnson 1961, Hamilton 1965, Hurly et al. 2001, Feo and Clark

2010). The sounds produced during these displays are either vocal (Clark 2006), or mechanically produced with their wings and/or tail (Clark and Feo 2008, 2010; Feo and Clark 2010).

Male Scintillant and Volcano hummingbirds have emarginated inner rectrices (Fig. 1) that may function to produce sound during displays (Stiles 1983), and male Scintillant have an emarginated P10 that may produce a wing trill (Stiles 1983). Our objectives in this paper are to: (1) describe the courtship displays and sounds of Volcano and Scintillant hummingbirds, and (2) provide natural history observations of their breeding biology.

METHODS

The Volcano Hummingbird presently has three recognized subspecies: *S. f. flammula*, *S. f. torridus*, and *S. f. simoni* (Stiles 1983). Most of our field work on this species was conducted on *S. f. torridus* in open fields and pasture surrounded by oak (*Quercus* spp.) forest near Estación Biológica Cuericí (09° 33' 11.90" N, 83° 40' 18.37" W; 2,600 m asl) and in Buenavista páramo habitat near km 89 on the Pan-American highway, east of San José (09° 33' 20.48" N, 83° 45' 18.63" W; 3,450 m asl), in the Cerro de la Muerte, Talamanca Mountains, San José Province, Costa Rica. We made additional observations and one sound recording of *S. f. flammula* on the summit of Volcán Irazú, Cartago Province (09° 58' 34.78" N, 83° 50' 57.63" W; 3,340 m asl) on 22 October 2009. We made observations of *S. scintilla* and *S. f. torridus* at the Quetzal Education and Research Center (QERC) in San Gerardo de Dota (09° 33' 1.55" N,

¹Peabody Museum of Natural History, Department of Ecology and Evolutionary Biology, Yale University, P. O. Box 208106, New Haven, CT 06511, USA.

²Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria Rodrigo Facio, 2060 San José, Costa Rica.

³Corresponding author; e-mail: christopher.clark@yale.edu

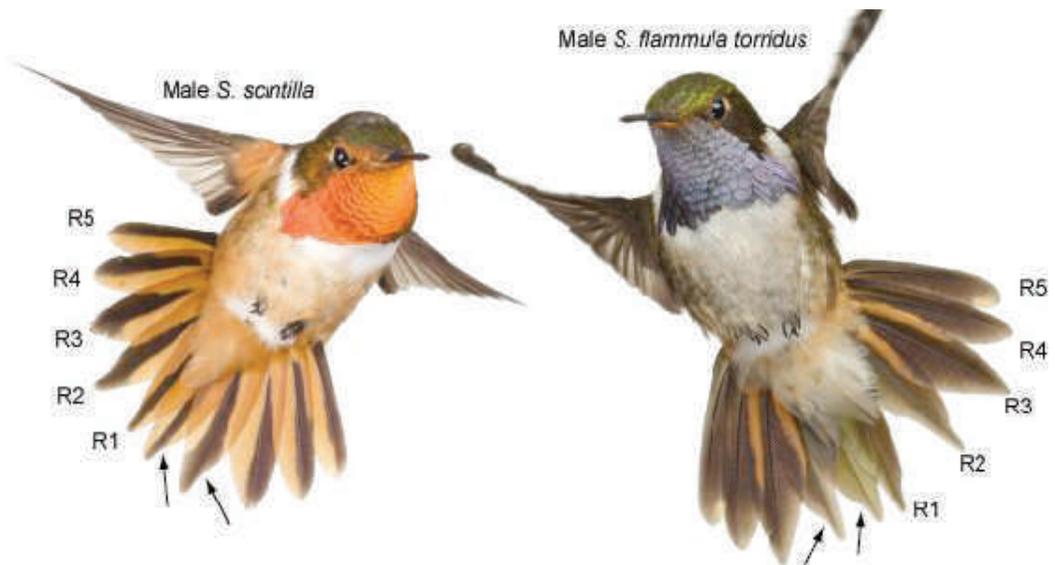


FIG. 1. Male Scintillant (*Selasphorus scintilla*) and Volcano (*S. flammula torridus*) hummingbirds with rectrices labeled R1–R5. R1 and R2 are emarginated in males (arrows). Emargination is more pronounced in the Volcano Hummingbird. Photographs courtesy Anad Varma.

83° 48' 26.01" W; 2,200 m asl), San José Province. All observations occurred between 12 and 22 October 2009.

We obtained high-speed videos of hovering and displaying hummingbirds with a hand-held monochrome high-speed camera (MIRO EX4, Vision Research, Wayne, NJ, USA) recording at 500 fps with a resolution of 800 × 600 pixels. We obtained sound recordings using a shotgun microphone (Sennheiser MKH70, Wedemark-Wennebostel, Germany) attached to a 24-bit recorder (Sound Devices 702, Reedsburg, WI, USA), sampling at 48 kHz. Recordings were imported into Raven 1.3 (www.birds.cornell.edu/raven) and converted into spectrograms using a 512-sample window (Hann function, 50% overlap), except where otherwise indicated. Acoustic frequencies and temporal rates presented represent the frequencies recorded by the microphone and were not corrected for Doppler shift caused by the birds' velocity.

We captured hummingbirds with either mist nets (24-mm mesh) or feeder-traps. Some recorded sounds were natural, and the remainder were elicited by placing a live female in a cage on a male's territory, or by releasing a recently-captured female onto a homospecific male's territory. Volcano females were released on a male Scintillant's territory a few times, due to a

scarcity of Scintillant females, but failed to elicit a response. We collected tail feathers for laboratory experiments, and we opportunistically obtained dive recordings from one male Volcano Hummingbird both before and after plucking his entire tail. More extensive manipulations of wild birds (as in Clark and Feo 2008, 2010; Feo and Clark 2010) were unfeasible as these experiments typically take a few weeks. Tail feathers from each species were tested in a wind tunnel to ascertain if they were capable of producing sounds similar to the dive sound. This tunnel will be described in a future publication. All measures are mean ± SD. Specimens associated with this research have been deposited in the Peabody Museum, Yale University. Sound recordings have been deposited in the Museum of Vertebrate Zoology, University of California, Berkeley, USA (accession # 14752), and videos have been deposited in the Macaulay Library (accession #'s ML65124 to ML65144), Cornell University, Ithaca, New York, USA.

RESULTS

Volcano Hummingbird

Breeding and Territorial Behavior.—We saw females gathering nesting material and located two active nests with females incubating eggs at Cuericí on 15 October 2009, indicating breeding

was underway at this locality. Neither nest appeared to be on a male territory. Males at Cuericí held densely packed territories in open shrubby pastures full of cultivated blackberry (*Rubus* spp.), near remnants of oak (*Quercus* spp.) forest. No territories were found in closed canopy forest, although both males and females visited flowers in these areas. Males at the páramo site held small territories at the crest of a hill. Territories were small with perches of males being within a 15×15 m area, and central perches of neighboring territories as close as 20 m. They were tightly packed as compared to related species (CJC, pers. obs.). The males perched in 3–10 prominent locations, such as power lines, tips of dead twigs protruding from the side of a lone tree, or the tip of the tallest cane within a bramble patch while on territory. Perches were 1 to 15 m from the ground, and tended to be in sunny locations. Males at times moved to shaded perches in rare periods of prolonged sun and elevated temperatures.

Most interactions we observed on the territories were between males. Intruding males would frequently fly onto another's territory. The owner would leave his perch and chase the intruder. The chase would often, due to the tight packing of territories, immediately encroach on a neighboring territory, and that bird would join the chase as well; if the chase then entered yet another male's airspace, he too would join the fray. The greatest number of birds we observed in such a chase was four, accompanied by a tremendous twittering. Males seemed most active on their territories when it was sunny, and arrived on their territories within half an hour of sunrise. In contrast, they departed their territories up to 2 hrs before sundown.

All territories had at least a few plants in flower from which we saw the birds feed. The males were seen visiting *Fuchsia paniculata*, cultivated *Rubus* spp., *Comarostaphylis arbutoides*, and the tiny flowers of *F. microphylla* on their territories at Cuericí. Both males and females were also observed visiting a dense patch of undefended *Centropogon* spp. in the understory of nearby oak forest. Males and females at San Gerardo both defended territories around small dense patches of flowering *F. paniculata* with both attacking other *S. flammula* as well as *S. scintilla* that intruded onto a territory. Territorial females at San Gerardo (2,200 m asl) were not observed engaging in any behaviors that would indicate breeding, such as gathering nesting material.

Vocalizations.—Males uttered a 'descending' call (Fig. 2A) as well as a twittering 'scolding' call (Fig. 2B) in agonistic interactions with other Volcano Hummingbirds. The calls produced were directed towards another individual; we did not observe undirected vocalizations (i.e., songs) from males on their territories. The descending call was also occasionally emitted towards (caged) females. It consisted of a single tone that started at 9.9 ± 0.41 kHz, and descended to 6.8 ± 1.4 kHz over the course of 1.9 ± 0.6 sec ($n = 18$ calls from 7 males).

Display Dives.—Males were frequently observed performing display dives throughout the day. Two of the males we observed would dive at a variety of passerine birds, if they perched prominently on the male's territory, as well as at other hummingbirds. Most males did not seem to be so indiscriminate, and were only observed diving to other Volcano Hummingbirds. It was often not possible to ascertain the gender of the recipient of the display. It was easy to elicit dives from male Volcano hummingbirds by placing a caged female on the male's territories; the majority of males responded to this stimulus by performing at least one dive.

We obtained sound recordings of 87 dives from 13 males. The dive sound consisted of two sounds: a frequency-modulated (FM) tone and a series of sound pulses (Fig. 2C). Males began producing the FM tone early in the dive, which at its initial frequency was 4.07 ± 0.21 kHz ($n = 85$), and it remained nearly constant pitch (acoustic frequency) for 0.43 ± 0.17 sec. It was then modulated up to 5.80 ± 0.34 kHz ($n = 87$) over the course of 0.05 sec, then gradually descended in pitch to a final frequency of 4.97 ± 0.31 kHz. The entire sound lasted 0.92 ± 0.20 sec ($n = 85$), and a harmonic was present in 85 of 87 dives. The FM tone was clearly not produced by the tail, for one male lacking his tail still produced this sound when diving (Fig. 2E).

The dive sound also included 2–5 pulses of sound (indicated by *p* in Fig. 2C). These pulses were produced at the bottom of the display, as the male flew over the target of the display (Fig. 2C), and lasted 17 ± 11 ms ($n = 76$). The pulses were produced 46 ± 9 ms ($n = 73$) apart; the overall rate at which these pulses were produced was 15.2 ± 1.2 Hz ($n = 76$).

Each pulse consisted of a broad-frequency swath of sound reaching up to ~ 12 kHz. A low fundamental frequency (0.82 ± 0.29 kHz, 66

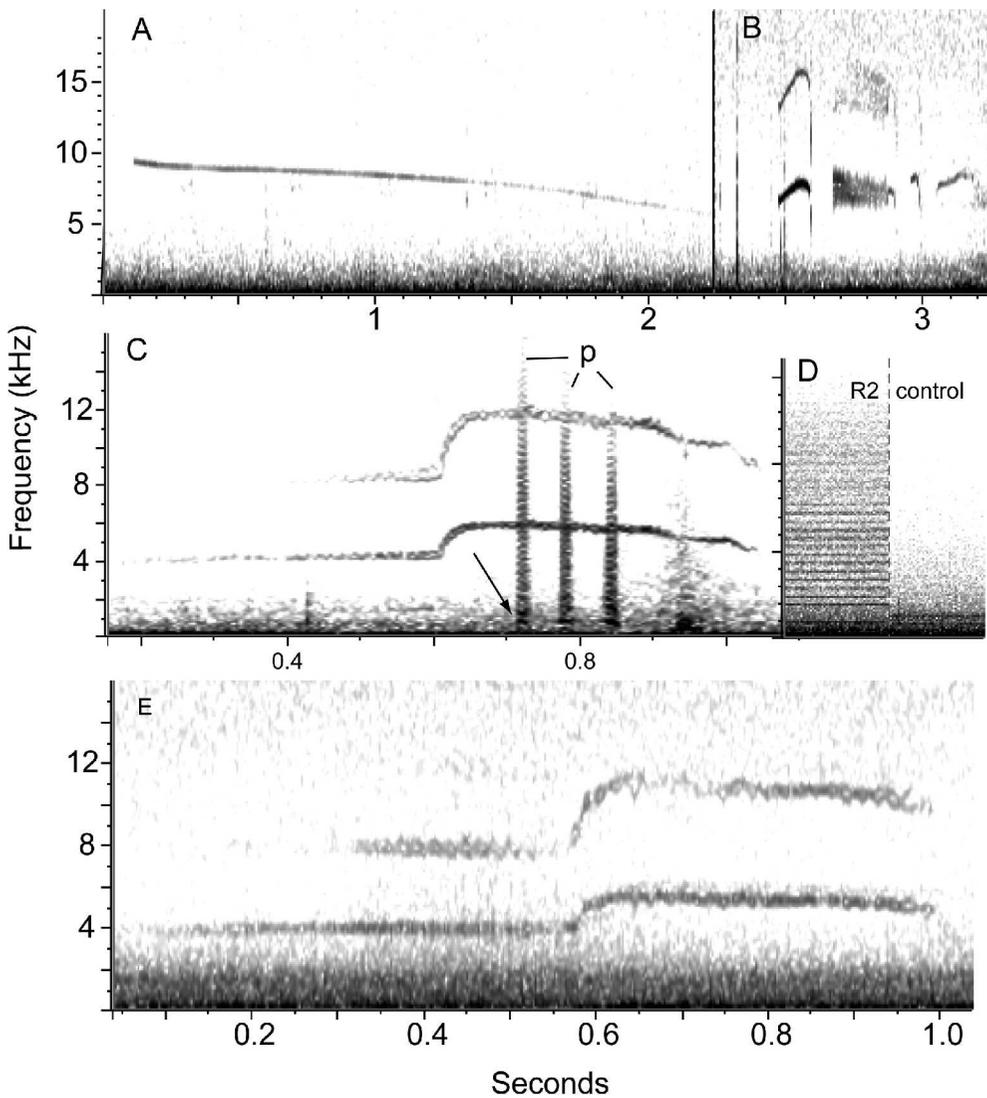


FIG. 2. Spectrograms of sounds produced by the Volcano Hummingbird. (A): descending call. (B): scolding call. (C): typical dive sound consisted of both the frequency modulated tone (FM) and low frequency sound pulses (p) with harmonic stack. Arrow indicates dominant frequency. (D): sound produced by a Volcano R2 in a wind tunnel set to 20 m/sec (left), and (right) tunnel control sound with same settings but no feather. Scintillant R2 produces essentially the same sound, but quieter. Spectrogram generated with a 2,048 sample window. (E): dive sound from a male missing his tail. The FM tone is present whereas the sound pulses are missing.

dives from 12 males; arrow in Fig. 2C) was present in 66 of 76 recordings. The sound appeared as a stack of many closely-spaced harmonic frequencies when analyzed using a spectrogram bin size of 2,048 samples (3 dB filter bandwidth: 34 Hz). The absence of the low frequency tone in 10 of the recordings may have been due to recording quality, such as recordings obtained further from the bird.

Dive Kinematics.—A male Volcano Hummingbird began a dive by ascending steeply with a slightly undulating trajectory (Fig. 3A). After rising ~25–30 m, he would turn and immediately dive, following a J or L-shaped path. After leveling out at the bottom of the dive, the male would use the accumulated speed to fly in a random direction, curving to the left or right, or up. If he performed a second dive, the male would

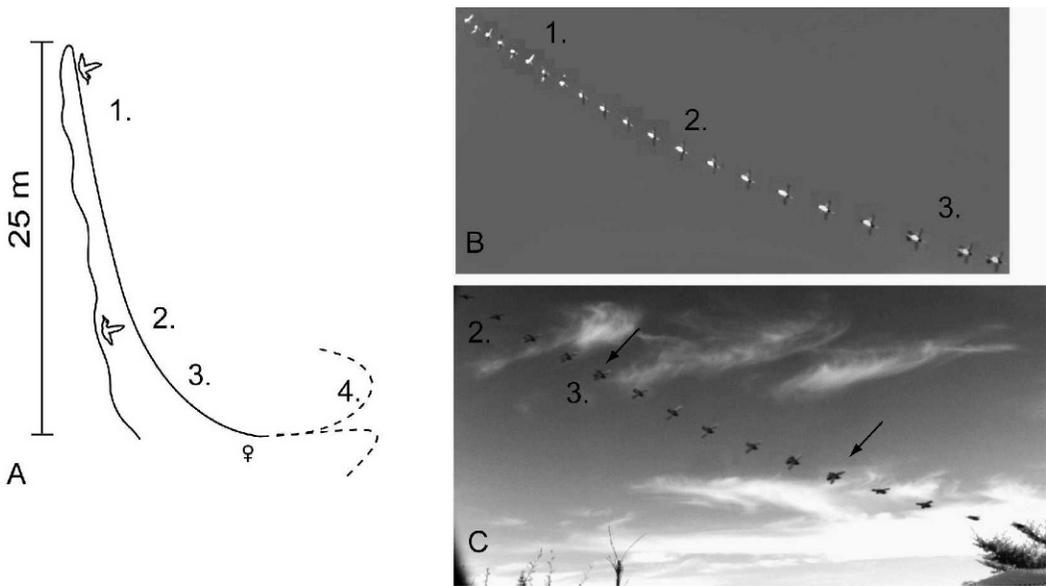


FIG. 3. Kinematics of display dive of the Volcano Hummingbird. (A): sketch of the dive with stages 1–3 labeled. Subsequent dives followed the same trajectory as the first dive. (B) and (C): composite images of diving birds from high-speed video. Consecutive images occurred 0.02 sec apart. Bird placement is approximate in both images, because the camera panned to follow the bird. (B): early in the dive in which the bird flapped its wings as it entered the frame (1.), then glided (2.), then spread its tail (3.) just as it left the frame. (C): the bottom of the dive in which the male spreads his tail multiple times (arrows).

re-ascend to the same starting position, and follow the same trajectory as the first dive, except for the variable ending (Fig. 3A). As a result, in consecutive dives the male passed over the recipient from the same direction. The direction of the dives did not seem to be specifically oriented towards the sun or another environmental feature that we could identify.

We obtained high-speed videos of parts of 15 dives, from seven different males. No single video showed the entire kinematic sequence of the dive. We identified stereotypical stages that appeared to be present in all of the dives by comparing the different videos. Each video was unique, thus sample sizes for each kinematic stage vary. Males descended in stage 1 (Fig. 3B) on flapping wings ($n = 8$ videos). They then ceased flapping and glided with tail shut (stage 2) for 0.17 ± 0.07 sec ($n = 4$ videos), before repeatedly spreading and shutting the tail while continuing to glide (stage 3; Fig. 3C). The tail was spread for 42 ± 9 msec ($n = 15$ spreads) and, from seven videos that showed more than one spread, the tail-spread frequency (the rate at which the tail was spread and shut) was 14.5 ± 1.6 Hz, which was not different from the sound pulse frequency (t -test, $P = 0.31$).

Male Volcano Hummingbirds during the dive had a wing-beat frequency of 58 ± 1.1 Hz ($n = 5$ high speed videos from 2 males). A caged male had a wing-beat frequency of 66.7 Hz, while a male hovering in the wild had a wing-beat frequency of 46.9 Hz; thus, the dive wing-beat frequency is within the range observed for hovering birds. Two caged females had a hovering wing-beat frequency of 42.7 ± 0.52 Hz. The wings did not make an audible wing trill during flight, and we did not observe any displays similar to the shuttle display of other *Selasphorus*.

We observed one or two male *S. f. flammula* perform about four dives on 21 October 2009, on the summit of Volcán Irazú, of which we obtained a sound recording from one individual. We did not detect dramatic differences in the dive trajectory from the kinematics described for *S. f. torridus* (Fig. 2), nor did we detect notable differences in the dive sound.

Scintillant Hummingbird

Breeding and Territorial Behavior.—We heard the wing trill of Scintillant Hummingbirds near food plants at Cuericí (2,600 m asl), and one male was collected at this location. We did not make

any behavioral observations of this species at Cuericí, and found no evidence of breeding at this location.

Scintillant Hummingbirds were breeding at San Gerardo (2,200 m asl). We observed females gathering nesting material and a female incubating a nest in a low bush on 13 October 2009. The nest did not appear to be on or near a male territory.

Males held territories in open areas such as the edge of an apple (*Malus* spp.) orchard, in a dense stand of blooming *Fuchsia paniculata*, or in short trees flanking a parking lot. All territories were in open areas, and males perched in 3–5 prominent locations between 2 and 15 m above the ground, on objects such as power lines, tips of dead twigs protruding from a large tree, on the tops of banana (*Musa* spp.) leaves, or the upper-most branches of a heavily blooming *Fuchsia*. All male territories contained at least a few plants in flower, and one included a hummingbird feeder.

The size of a territory varied depending on the amount of available food. Three males held densely-packed territories in a thick patch of blooming *F. paniculata* with all of the male's perches in a roughly 10×10 m area. These territories were also immediately adjacent to feeding territories held by both male and female Volcano Hummingbirds. Four territories found elsewhere, in areas with fewer natural food resources and fewer neighboring territories, were roughly 25×25 m in extent.

Natural dives were performed to female Scintillant Hummingbirds, or to hummingbirds of unknown gender. A female Scintillant repeatedly visited flowers on a male's territory during a set of natural observations spanning ~5 min. The male performed two sets of three dives to the female, and spent the rest of the time watching her while occasionally producing a type *a* call, or chasing her. Male Scintillant and both male and female Volcano hummingbirds that entered the males' territories were scolded and chased. In general, the behavior of the territorial males seemed similar to that of male Rufous and Allen's hummingbirds, in terms of activity, vocalizations, and tendency to engage in aggressive interactions with other hummingbirds (CJC, pers. obs.).

Vocalizations.—Males did not sing undirected song from their perches. They did produce at least three types of calls, two of which are labeled *a* and *b* (Fig. 4A). A third, apparently agonistic (scolding) call was produced, often while perched,

and sounded similar to a call produced by Allen's and Rufous hummingbirds. We did not obtain a clear recording of this call. Both males and females at times produced call *a* in the apparent absence of other hummingbirds, while the other two calls seemed to be produced only in agonistic interactions.

Wing Sounds and Shuttle Display.—Male Scintillant Hummingbirds produced a distinctive wing trill during flight (acoustic frequency: 9 kHz; Fig. 4B) that sounded nearly identical to the wing trill of Allen's and Rufous hummingbirds. Males also produced a shuttle display characterized by distinctive sounds and flight kinematics similar to the shuttle displays performed by Allen's and Rufous hummingbirds. The shuttle displays had two variants, 'stationary' and 'traveling'. A male repeatedly approached a female in a cage and then produced a stationary shuttle, in which he flew back-and-forth while producing the sound. This variant was also heard emanating from inside of a bush into which a male had pursued an unidentified hummingbird. In the second variant, males ($n = 2$) that spotted a female crossing their territory would leave their perch and pursue the female, but not at their top speed. In this traveling shuttle, as they followed the female, the males would occasionally produce the shuttle display sound, visually appearing to decrease their forward flight speed and change their wing beat kinematics as they did so.

We obtained five sound recordings from two males performing the shuttle display (Fig. 4D). Males produced similar sounds during the traveling and stationary variants of the shuttle display. The shuttle display sounds consisted of repeated sounds that appeared in alternating duplets. One pair of sounds matched the acoustic form of the male's wing trill (i.e., sound pulses with a mean acoustic frequency of 9.4 ± 0.43 kHz and a frequency bandwidth of 1.87 ± 0.28 kHz; $n = 5$; labeled *w* in Fig. 4D). The alternate duplet (*s* in Fig. 4D) was a broad-band sound without a single discrete frequency. The trill rate was 93.8 ± 5.1 Hz ($n = 5$).

High-speed videos of four shuttle displays from one male were recorded. The male was partially obscured behind other objects or, at times, out of frame throughout most of the videos, and sample sizes of specific events vary. The male flapped his wings at 98.1 ± 2.64 Hz ($n = 4$ displays) during the shuttle display, while rhythmically moving his body. We term each repeated, rhythmic move-

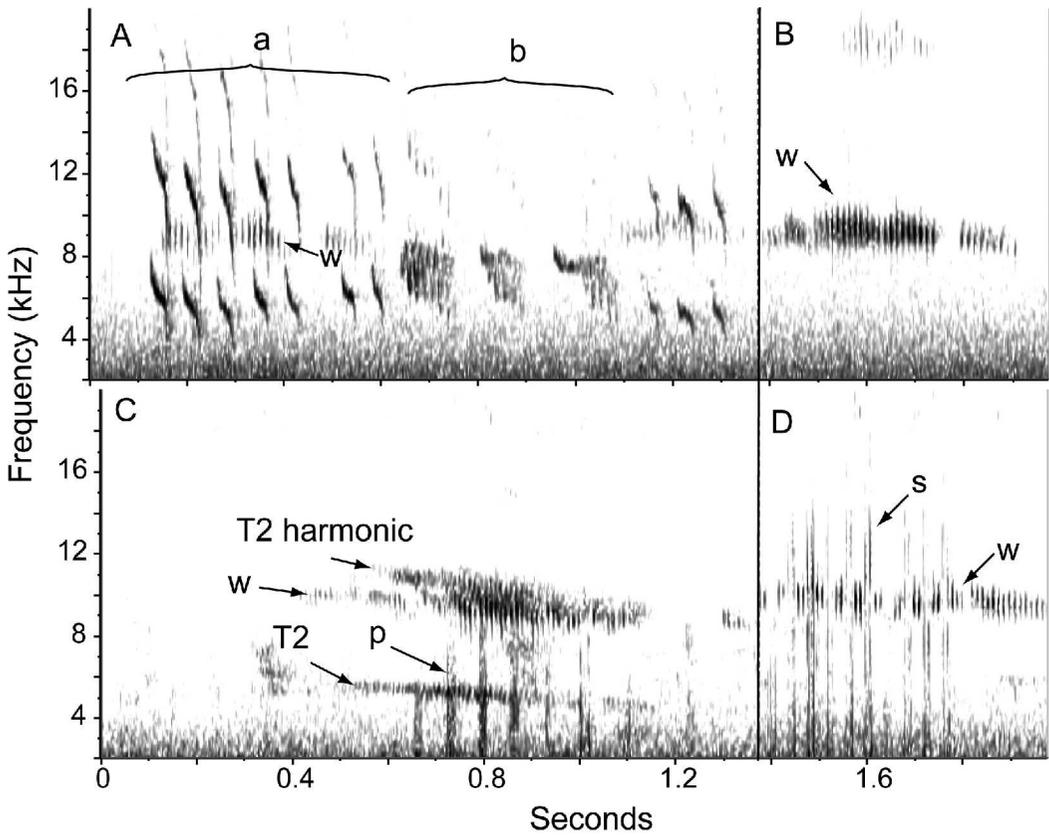


FIG. 4. Spectrograms of sounds produced by Scintillant Hummingbirds. (A): two types of vocalizations, *a* and *b*. Wing trill (*w*) of male is also present. (B): wing trill (*w*) produced by adult males. A faint harmonic is present. (C): dive sound consisted of the wing trill (*w*), an additional trill (T2), a harmonic of the additional trill, and a sound pulse (*p*). At least four sound pulses are present. The pulses are produced at the bottom of the dive, as the male passes over the female. (D): a stationary shuttle display to a female in a cage, which consisted of alternating duplets of sounds. One duplet comprises the wing trill (*w*), alternating with duplets of sound *s* that are broadband.

ment an individual 'shuttle motion'. Twice, the stationary shuttle display was performed to a female in a cage: with gorget flared, the male shuttled from side to side (laterally) in front of the cage, over a horizontal distance of ~ 20 cm. The male would abruptly roll his body (i.e., rotate around his longitudinal axis) while arresting his lateral motion at the end of each shuttle, flap his wings with asymmetrical motions, and sweep his tail sideways through a range of angles. The wings did not appear to strike each other or anything else, during these motions.

The other two high-speed videos were of the traveling shuttle display. Unlike the stationary shuttle, in which the male tended to fly side-to-side (laterally) repeatedly through the same space, during the traveling shuttle, the male was

continually flying forward towards the female with little lateral motion. During this forward flight the male engaged in periodic body rotations, tail rotations, and asymmetrical wing kinematics similar to the stationary shuttle display (Fig. 5A). Shortly after finishing one shuttle motion, the bird would start another, rotating its body and tail in the opposite direction from the previous. The total time spent rotating the tail was 73 ± 9 msec ($n = 5$ shuttles from 2 videos); the timing between shuttle motions was 55 ± 13 msec ($n = 2$ intervals). Therefore, the rate at which shuttle motions were performed was 7.8 Hz. No component of the shuttle sound was produced at a rate of 7.8 Hz, and this striking visual component of the display kinematics did not appear to correspond to production of a single particular sound.

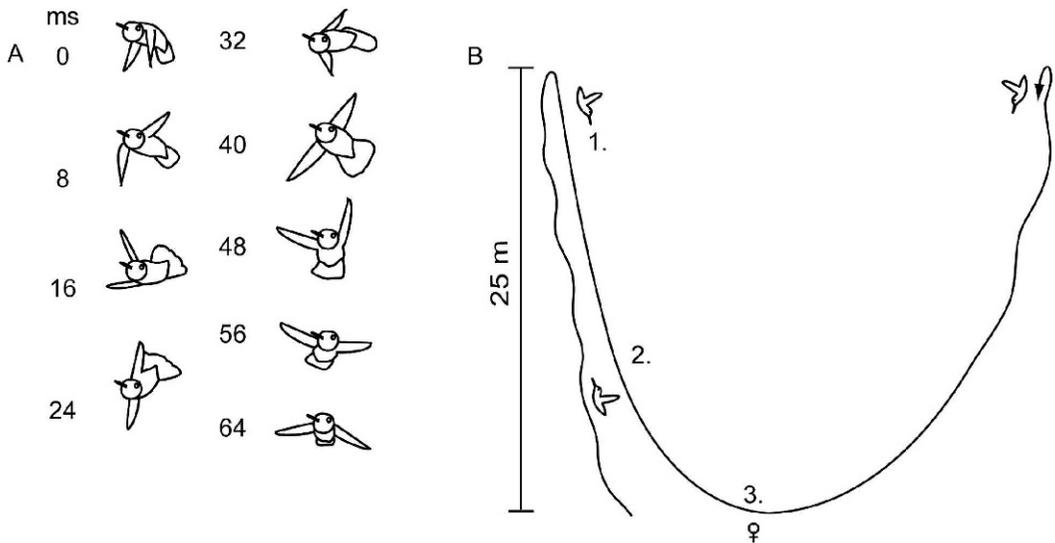


FIG. 5. Shuttle and dive display kinematics of the Scintillant Hummingbird. (A): sketch of the traveling shuttle display, traced from frames of a high-speed video. Tracings are of the bird's posture (each wing, head, body, and tail) every 8 ms. The male was flying towards the camera with little lateral motion. Initially, the bird was flying towards the camera while the wings flapped symmetrically and the body's roll angle was nominally zero (0 ms). At 8–24 ms, the wing motions abruptly became asymmetric (i.e., the wings differed in stroke amplitude, stroke angles, and moved out-of-phase by up to 90°), and the tail was abruptly spread and twisted up and to the bird's left, while the body's roll angle rotated to $\sim 90^\circ$ (left side down; bird's ventral side towards camera). The spread tail proceeded to sweep around rapidly (24–48 ms) from left to right, and towards the end of this motion the bird's roll angle returned to 0° . The wings returned to flapping symmetrically (56–64 ms) at the end of the shuttle. The wings did not appear to strike any part of the bird's body during these motions, and six wing beats occur within the 64 ms depicted. (B): sketch of the dive trajectory with stages 1–3 labeled. Males undulated slightly as they ascended. Stage 1: flapping with tail shut, 2: gliding with tail shut, 3: flapping and spreading tail. Stage 2 is only present in some dives. Subsequent dives were in the opposite direction from previous dive.

Display Dives.—Male Scintillant Hummingbirds would approach a caged female, but this did not elicit dives ($n = 3$ males), similar to territorial male Allen's and Rufous (CJC, pers. obs.). We recorded natural dives from one male, and elicited dives from two males by releasing a Scintillant female on territory. The male would perform a shuttle display, followed by 1–6 dives, to females that landed in his territory. We recorded sounds of 17 dives from three males.

The primary audible sound during the dive was the sound of the wing trill. Two additional faint sounds were present in seven good sound recordings (Fig. 4C). The dive began with the wing trill produced at a rate of 92.5 ± 1.9 Hz ($n = 17$). There was a gap lasting 0.32 ± 0.12 sec in production of the trill early in the dive in seven of 17 dives. Two to six faint pulses (p in Fig. 4C) of sound were produced ($n = 7$ dives) at the bottom of the dive at a temporal rate of 16 ± 2.7 Hz ($n = 7$). An additional trill appeared (trill 2 in Fig. 4C) at the same time these pulses were produced with

an average pitch ranging from 5.3 to 5.4 kHz and a bandwidth of 0.76 kHz ($n = 16$). Trill two had a harmonic that was slightly higher in pitch than the wing trill.

Males began a dive by ascending on a slightly undulating path to a height of ~ 25 m (Fig. 5B). The male would then turn and dive at a steep angle, swooping directly over the female and then rise again, tracing a giant U. At the end of the first dive the male would then turn and perform the next dive, following the same path but in the opposite direction from the previous dive, in the same vertical plane.

We obtained high-speed videos of part of four dives from two males. All lost the bird partway through the bottom of the dive. Males began the dive by powering their descent with flapping wings (stage 1). Males continuously flapped for the entire dive in three dives while in the fourth the male briefly switched to a glide (stage 2). Males repeatedly spread and shut their tail at the bottom of the dive while continuing or resuming

flapping. The males spread the tail four times in two videos, and two times in the other two videos. The videos looked similar to those shown for the Volcano Hummingbird in figures 3B–C, except the wings were flapped at the nadir of the dive. The tail was spread for an average of 37 ± 2 msec ($n = 7$ spreads), and the intervals between spreads were 31 ± 3 msec ($n = 6$), resulting in a tail spread cycle rate of 14.7 Hz—corresponding to that at which the pulses of sound were produced. The gliding phase (stage 2) apparently explains the gap in production of the trill during the dive in some of the dive recordings. The dive wing beat frequency was 93.7 ± 0.66 Hz, matching the wing trill rate during the dive. Two male *S. scintilla* had a mean wing-beat frequency of 68.9 ± 7.6 Hz while hovering in a cage.

The R2 of both the Scintillant and the Volcano hummingbirds, when placed in a wind tunnel at speeds of 10–20 m/sec, produced sounds at the same frequencies as the pulsed sounds that the birds make while diving (Fig. 2D). The feathers generate tones with a fundamental frequency ranging from 0.3 to 0.5 kHz (depending on air speed), but in which the second or third harmonic is dominant. The feathers in the wind tunnel generated a stack of 20 or more harmonics, similar to the broad swath of sound present in the sound pulses (Figs. 2, 4). In particular, the emarginated tip of the feather flutters to generate the sound.

DISCUSSION

Our observations provide new information about the natural history of Scintillant and Volcano hummingbirds. The shuttle display of the male Scintillant, and dive displays produced by both species appear to be courtship displays. We saw males of both species naturally display to females, when a female was on a male's territory. Males rarely displayed to other males, tending to chase or ignore them instead. Our experimental use of homospecific females was sufficient to immediately elicit displays from males, whereas *S. flammula* females released on a *S. scintilla*'s territory were ignored.

Our goal in conducting this research was to investigate whether *Selasphorus* species produce sounds with their wings and tail feathers. The tonal, FM portion of the Volcano Hummingbird's dive sound is not produced by the tail (Fig. 2E), and is likely vocal. In contrast, the pulses of sound produced during the dive of both species are timed

to the rapid tail-spreads in both species. We found similar one-to-one correspondences between kinematics and tail-generated sounds in Anna's (*Calypte anna*), Black-chinned (*Archilocus alexandri*), and Calliope hummingbirds (Clark and Feo 2008, Clark 2009, Feo and Clark 2010). Moreover, the emarginated R2 (Fig. 1) of each species can generate sounds matching the dive sounds when placed in a wind tunnel (Fig. 2D). Rufous and Broad-tailed hummingbirds produce similar sounds during their dives, and both of these species also have emarginated inner rectrices (Stiles 1972, 1983), similar to Volcano and Scintillant hummingbirds (Fig. 1). We hypothesize that all of these species produce similar sounds during their dives via fluttering of the emarginated tip of R2.

There is also a one-to-one match between video and sound recordings of the Scintillant Hummingbird's shuttle display. Sound elements *w* and *s* were produced cumulatively at a rate of 93.8 ± 5.1 Hz, closely similar to the measured wing-beat frequency of 98.1 ± 2.64 Hz. We conclude that *w* and *s* are produced by the wings, but how this is done is unclear for two reasons. First, although the individual shuttle motions of the shuttle display were periodic, they were produced at a frequency of 7.8 Hz. This is nearly four times slower than the rate of 27.8 Hz (the rate at which a cycle of a *w* duplet and *s* duplet were produced); thus, four cycles of such sounds were produced during each shuttle motion. We did not discern specific wing motions associated with the *s* elements. Second, the *s* elements are so short in duration that the sound spectrogram is intrinsically of limited use in detecting if they are truly atonal (broadband), or whether they represent a stack of closely-spaced harmonics, like the sound pulses of the dives. If they are harmonic stacks, perhaps they are produced via some form of resonant flutter (Clark and Feo 2008). If they are truly broadband, this would suggest they are produced by another mechanism such as percussion (Bostwick and Prum 2003) or rubbing (Bostwick 2006).

The function of male Volcano Hummingbird territories is not entirely clear. Wolf and colleagues (Wolf 1976, Wolf et al. 1976) called them feeding territories, implying that males were guarding a space specifically according to the value of the food resources it contained. But, food resources seemed nearly ubiquitous at our study sites, such that it would be difficult to find an open space that did not have some food present.

Thus, the presence of food on a territory is not evidence that it is a feeding territory. Some of the densest food resources (blooming *Fuchsia*, *Centropogon*) that occurred in closed canopy appeared to be undefended, whereas we only observed territories in open areas. In the related Anna's and Calliope hummingbirds, males will hold breeding territories in the absence of food (Tamm 1985, Armstrong 1987, Powers 1987, Tamm et al. 1989), and even those holding a territory with food resources tend to have less food available than nearby undefended locations (Armstrong 1987). We suggest that breeding male Volcano Hummingbirds are not guarding territories for the floral resources that they contain.

Males could also hold territories to guard resources other than flowers, such as insects (for which females have high demand when breeding) or nesting sites. Females did not seem to nest on male territories. It is possible they visited territories of males to obtain resources such as nectar or insects (Temeles and Kress 2010), but we made no direct observations that would support this idea. Our interpretation of the Volcano Hummingbird's territoriality is that males need open areas to perform the display dive, and the primary function of the territory is courtship, making the mating system most similar to an 'exploded' lek.

The function(s) of the territories of male Scintillant Hummingbirds were less clear. The six males we found all had ample food resources on their territories, and defended their territories from Volcano Hummingbirds (nectar competitors) and male Scintillant alike, similar to the interspecific territoriality of breeding male Anna's and Allen's hummingbirds (Pitelka 1951). Moreover, a female was seen extensively feeding on one of these territories, although she did not appear to reside there. These observations suggest that resources have a role in the territory ownership of these males, perhaps more so than for Volcano Hummingbirds.

However, as for the Volcano Hummingbird, all six of these territories were held in open areas. Dense patches of flowers in areas with greater forest canopy cover had many male and female Scintillant Hummingbirds visiting them, but we did not detect any male territories in these closed areas. It is possible the males visiting these flowers were not holding territories but, as males of related species are known to forage away from their breeding territories (Armstrong 1987; Powers 1987; CJC,

pers. obs.), we suspect the males we observed at these flowers held a territory elsewhere, and were commuting from their territories to feed. If true, we hypothesize that, as in the Volcano Hummingbird, habitat structure is more important than food availability for territory location. This hypothesis could be tested by covering or removing the flowers on male territories (e.g., Armstrong 1987) to examine if territorial behavior is maintained in the absence of floral resources. The potential difference in the importance of food on breeding territoriality between the Scintillant and Volcano hummingbirds would make for an interesting comparative study.

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